

AGE AND SEX DIFFERENCES IN THE TIMING OF FALL MIGRATION OF HAWKS AND FALCONS

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ABSTRACT.—We trapped more than 23,000 migrating raptors at Cedar Grove, Wisconsin during the autumns of 1953–1996, permitting accurate identification of age and sex. Adults migrated significantly later than juveniles in 8 of 10 species, and males migrated later than females in 7 species. We suggest that it is adaptive for adults and males to remain on breeding territories as long as possible. Adult Peregrine Falcons (*Falco peregrinus*) migrated before juveniles. There was no age difference in migration of Rough-legged Hawks (*Buteo lagopus*). Both species breed in the Arctic where the brief breeding season requires that adults leave as soon as possible so adults might then migrate more rapidly than juveniles. We compare our results with those of 16 other studies. Juveniles migrated significantly later than adults in 8 of 13 species at Falsterbo in southern Sweden (Kjellén 1992). Falsterbo is more than 12° latitude (1300 km) north of Cedar Grove and the breeding range of most of the species occurring there extends north of the Arctic Circle, where birds suffer from the same abbreviated breeding seasons as do the Peregrine Falcon and Rough-legged Hawk in North America. Adult females migrated after adult males in the two large species of *Accipiter*; this may be because the females, not the males, establish and maintain territory in these species. Received 16 April 1999, accepted 13 Feb. 2000.

It has been known for more than 60 years that there are age and sex differences in winter distribution and the timing of migration of birds (Eaton 1933, Nice 1937). Relatively few studies have provided data on the differences occurring during fall migration. Kerlinger (1989) listed 7 hypotheses that have been proposed to explain age or sex differences in the timing of migration or the wintering areas of birds: (1) The migration threshold hypothesis (Baker 1978) is an all inclusive, complex multifactorial approach, probably including all of the other hypotheses. This hypothesis is untestable (Ketterson and Nolan 1983), hence it cannot be falsified and it makes no predictions. (2) The character divergence hypothesis (Koplin 1973) explains habitat segregation in wintering birds as a mechanism to avoid competition between the sexes. But this merely substitutes intrasexual competition for intersexual and is possible only if one invokes group selection (Jehl 1970, Mueller 1990); it also makes no predictions. (3) The arrival time hypothesis (King et al. 1965, Myers

1981) predicts that the sex engaged in intrasexual competition for access to mates would migrate earlier in spring and winter closer to the breeding area, but it makes no predictions for fall migration. (4) The physiological hypothesis (Ketterson and Nolan 1976) states that large birds are better able to withstand the rigors of northern winters and thus winter farther north, and by extension, migrate later in fall. Female raptors are larger than males and thus would be expected to migrate later in fall. (5) The social dominance hypothesis (Mueller et al. 1977, Gauthreaux 1978) holds that the larger sex forces the smaller sex to migrate farther and earlier in autumn. Males are the smaller sex in raptors. (6) The molt hypothesis (Smallwood 1988) holds that males migrate after females in autumn because males molt remiges later than females, but only adults molt and this fails to explain sex differences in juveniles. (7) The feeding efficiency hypothesis (Rosenfield and Evans 1980) maintains that juveniles migrate earlier than adults because they are less efficient predators and migrate earlier along with most of their avian prey. Females also migrate before males because the larger prey they hunt more efficiently is scarcer than the smaller prey that is optimal for males, and as the season progresses and more prey birds migrate south, larger prey become even more scarce. We add an eighth hypothesis: young birds migrate earlier than

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adults because of their inexperience in finding a wintering home.

Capturing a hawk during migration permits accurate determination of age and sex. In this paper, we examine data gathered in routine hawk trapping during fall migration in south-eastern Wisconsin, compare our results with other studies, and evaluate the various hypotheses.

METHODS

We trapped 23,745 diurnal raptors of 17 species in the autumns of 1953–1996 at the Cedar Grove Ornithological Station (43° 33' N, 87° 21' W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin. Sufficient individuals were obtained to distinguish age and sex differences in timing of migration in 8 species and on sex differences in juveniles in 2 additional species.

Sex was determined by plumage in the American Kestrel (*Falco sparverius*), adult male Northern Harriers (*Circus cyaneus*), and adult male Merlins (*Falco columbarius*). Measurements were used to determine sex in juvenile Northern Harriers (Bildstein and Hamerstrom 1980), Northern Goshawks (*Accipiter gentilis*; Mueller et al. 1976), Cooper's Hawks (*A. cooperii*; Mueller et al. 1981), Sharp-shinned Hawks (*A. striatus*; Mueller et al. 1979), Merlins (*Falco columbarius*; Clark 1985a), and Peregrine Falcons (*F. peregrinus*; Ratcliffe 1980). Sex was not determined in Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*B. lineatus*), and Rough-legged Hawks (*B. lagopus*), but an estimate of sex was obtained by dividing the distribution of hawks trapped into large and small halves based on measurement of wing chord. Age was determined by plumage. Birds with juvenile plumage were classified as HY (hatching year). Many hawks and falcons have not completed their molt during fall migration and the presence of two generations of feathers permits the separation of some adults into SY (second year) and ASY (after second year). Where sample sizes of SY and ASY birds were small we grouped them into AHY (after hatching year) as we did with the adults of species where SY or ASY could not be determined. We began to record molt and the exact plumage of adults consistently in 1962.

The extent of the breeding range to the north of Cedar Grove, and the northernmost and southernmost extent of the wintering range were obtained from Palmer (1988). The same information for Swedish raptors was obtained from Beaman and Madge (1998). The maximum distance of migration is the difference from the northernmost extent of breeding to the southernmost extent of wintering range.

The Mann-Whitney *U*-test was used to compare the timing of migration of age and sex groups. Sample sizes are given in Fig. 1. Comparisons of the proportion of birds trapped early and late in the season were performed with a 2×2 χ^2 test, utilizing Yate's cor-

rection. The Fisher exact test was used in one case where sample sizes were too small for χ^2 analysis. Statistics were performed in SYSTAT (Wilkinson 1989) on a MacIntosh computer.

We used several different kinds of traps and lures to capture the raptors, and sex ratios of many species attracted to the traps vary with trap and lure type. The types of traps and lures used varied over the 44 years of the study and a simple analysis of the bias of sex ratios is impossible. Consequently, the data should not be used to estimate sex ratios in nature.

RESULTS

Northern Harrier.—HY birds migrated before AHY (Fig. 1, Table 1). AHY males tended to migrate after AHY females ($P = 0.08$), there was no sex difference in the timing of HY birds. Only 12% of the AHY were identified as SY or ASY; the small samples precluded an examination of differences between the two. More than 7% of the Northern Harriers observed on or before 12 October were trapped, but only 4% of those observed after this date were captured, indicating that AHY are more difficult to trap than HY ($\chi^2 = 28$, 0.001).

Northern Goshawk.—HY hawks migrated before SY and ASY (Fig. 1, Table 1), but there was no difference in timing between SY and ASY in either sex. The only difference between the sexes was between ASY females and males; females migrated later than males. The median date for both males and females was 5 November. We trapped 31 males and 25 females on this date. Essentially half (112 of 225) of the males were captured on or before 4 November; only 42% of the females (86 of 204) were captured on or before 4 November. Only 36% of the males were caught on or after 6 November; over 45% of the females were trapped during this interval. The percentage trapped (57%) remained approximately constant throughout the season, suggesting that AHY were trapped as readily as HY.

Cooper's Hawk.—SY birds migrated later than HY (Fig. 1, Table 1) and ASY migrated later than SY ($P < 0.01$, both sexes). HY males migrated later than HY females, but both SY and ASY females migrated later than males. AHY birds appear to be trapped as readily as HY.

Sharp-shinned Hawk.—SY hawks migrated later than HY (Fig. 1, Table 1), and ASY later than SY. Males migrated later than females.

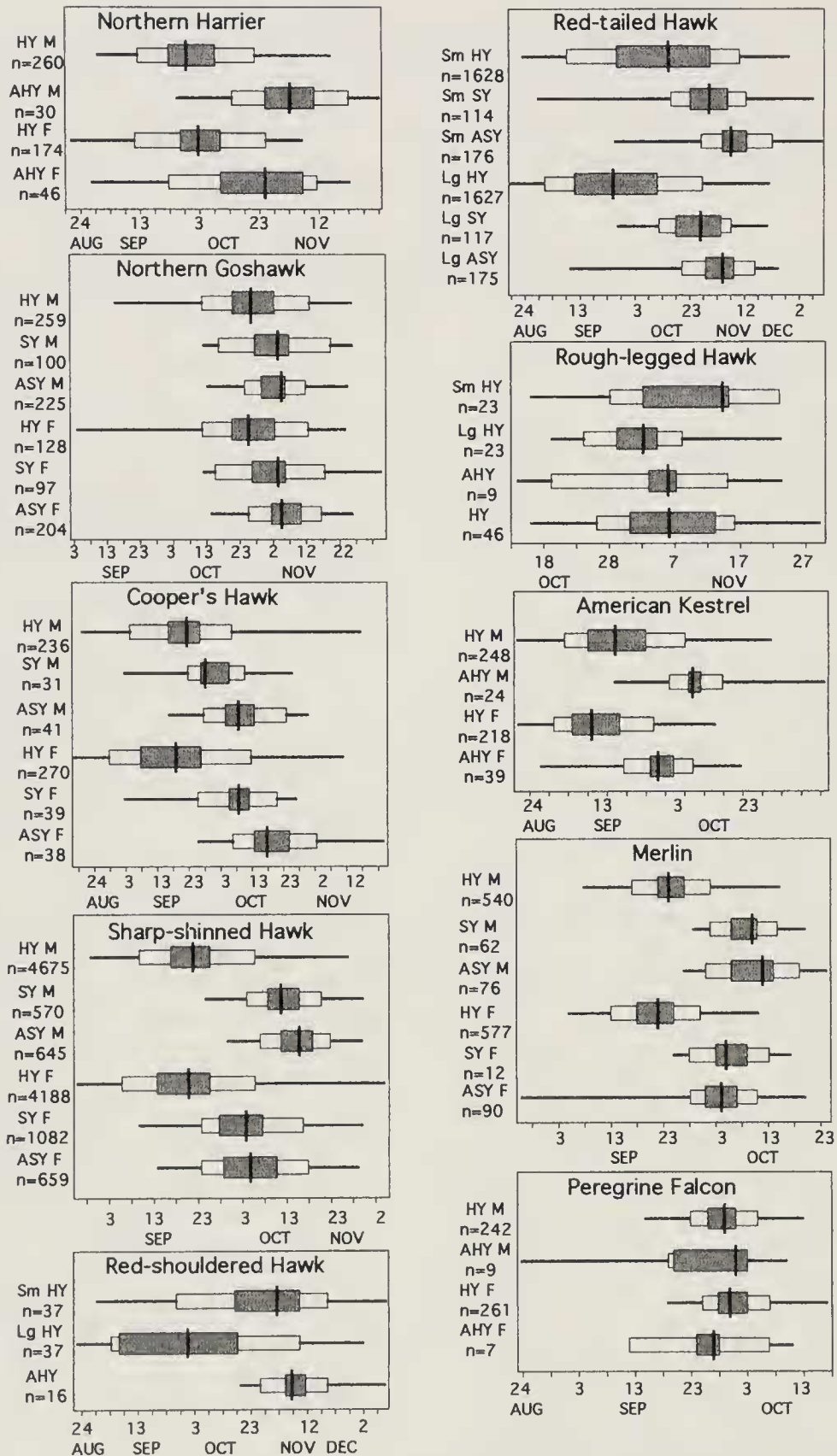


FIG. 1. Temporal distribution of hawks and falcons in autumn migration. HYM: Hatching year males (males in the juvenal plumage). SYM: Second year males (males in first basic plumage with some juvenal feathers). ASYM: After second year males (males with feathers from two basic plumages). AHYM: After hatching year males (males two or more years old). F: females. Sm: Birds with wing chords shorter than the mean. Lg: Birds with wing chords longer than the mean. The vertical line indicates the median date, the shaded bar, $\pm 16.7\%$ of the birds trapped, the white bar, an additional $\pm 16.7\%$, and the horizontal line, an additional $\pm 14.5\%$. The three categories thus include 33%, 67% and 95%, respectively.

TABLE 1. Results of Mann-Whitney *U* tests on age and sex differences in timing of migration.

Species	Comparison	Sample sizes	<i>U</i>	<i>P</i>
Northern Harrier	HY vs AHY males	259, 31	11,245	<0.001
	HY vs AHY females	172, 46	2136	<0.001
	AHY males vs females	31, 46	884	0.08
	HY males vs females	259, 172	21,618	>0.05
Northern Goshawk	HY vs SY males	259, 100	9963	<0.001
	SY vs ASY males	100, 225	11,587	>0.05
	HY vs SY females	128, 97	4915	<0.01
	SY vs ASY females	97, 204	8761	>0.05
	HY males vs females	259, 158	16,722	>0.05
	SY males vs females	100, 97	4980	>0.05
	ASY males vs females	225, 204	19,478	<0.01
Cooper's Hawk	HY vs SY males	236, 31	2532	<0.01
	SY vs ASY males	31, 41	374	<0.01
	HY vs SY females	270, 39	2715	<0.001
	SY vs ASY females	39, 38	383	<0.001
	HY males vs females	236, 270	34,807	0.05
	SY males vs females	31, 39	428	<0.05
	ASY males vs females	41, 38	457	<0.01
Sharp-shinned Hawk	HY vs SY males	4675, 570	151,839	<0.001
	SY vs ASY males	570, 645	141,195	<0.001
	HY vs SY females	4188, 1082	272,150	<0.001
	SY vs ASY females	1082, 659	332,866	<0.05
	HY males vs females	4675, 4188	823,588	<0.001
	SY males vs females	570, 1082	450,556	<0.001
	ASY males vs females	645, 659	328,525	<0.001
Red-tailed Hawk	Sm HY vs Sm SY	1628, 114	123,532	<0.001
	Sm SY vs Sm ASY	114, 176	6913	<0.001
	Lg HY vs Lg SY	1627, 117	14,579	<0.001
	Lg SY vs Lg ASY	117, 175	6954	<0.001
	Sm vs Lg HY	1628, 1627	1,681,435	<0.001
	Sm vs Lg SY	114, 117	7586	<0.05
	Sm vs Lg ASY	176, 175	18,574	<0.001
Red-shouldered Hawk	Sm vs Lg HY	37, 37	929	<0.01
	HY vs AHY	74, 16	339	<0.01
Rough-legged Hawk	Sm vs Lg HY	23, 23	367	<0.05
	HY vs AHY	46, 9	206	>0.05
American Kestrel	HY vs AHY males	248, 24	829	<0.001
	HY vs AHY females	218, 39	1652	<0.001
	AHY males vs females	24, 39	748	<0.001
	HY males vs females	248, 218	32,902	<0.001
Merlin	HY vs SY males	540, 62	3001	<0.001
	SY vs ASY males	62, 76	2732	>0.05
	HY vs SY females	577, 12	627	<0.001
	SY vs ASY females	12, 90	652	>0.05
	HY males vs females	540, 577	128,407	<0.001
	SY males vs females	62, 12	444	>0.05
	ASY males vs females	76, 90	4950	<0.001
Peregrine Falcon	HY vs AHY males	242, 9	1073	>0.05
	HY vs AHY females	261, 7	1126	>0.05
	AHY males vs females	9, 7	33	>0.05
	HY males vs females	242, 261	26,024	<0.001

Almost 22% of the Sharp-shinned Hawks observed on or before 30 September were trapped, but only 14% of those seen after this date were captured, indicating that AHY are more difficult to trap than HY ($\chi^2 = 684$, $P < 0.001$).

Red-tailed Hawk.—SY hawks migrated later than HY (Fig. 1, Table 1) and ASY later than SY. Small birds migrated later than large birds. Almost 26% of the Red-tailed Hawks observed on or before 4 October were trapped, but only 12% of those seen after this date were captured, indicating that AHY are much more difficult to capture than HY ($\chi^2 = 463$, $P < 0.001$).

Red-shouldered Hawk.—AHY hawks migrated later than HY (Fig. 1, Table 1). We were able to assign only 3 adults to SY or ASY. Small HY hawks migrated later than large HY; the sample of AHY was too small for analysis. More than 12% of the Red-shouldered Hawks observed on or before 19 October were trapped, but only 4% of those seen after this date were captured, indicating that AHY are much more difficult to trap than HY ($\chi^2 = 22$, $P < 0.001$).

Rough-legged Hawk.—Although only 9 AHY were captured, the lack of even a hint of a difference (Fig. 1, Table 1) in timing of migration between adults and juveniles suggests that there is no difference. Small juveniles migrated later than large juveniles.

American Kestrel.—AHY kestrels migrated later than HY (Fig. 1, Table 1), and males migrated later than females. We trapped almost 13% of the American Kestrels observed before 22 September, but only 7% of those observed after this date, indicating that AHY are more difficult to capture than HY ($\chi^2 = 37$, $P < 0.001$).

Merlin.—SY adults migrated later than HY (Fig. 1, Table 1), but there was no significant difference in timing between ASY and SY. HY males migrated later than HY females and ASY males migrated later than ASY females, but there was no significant difference between the sexes in SY, although the sample is small for females. We trapped almost 16% of the Merlins observed before 29 September and less than 4% of those seen after this date, indicating that adults are much more difficult to capture than juveniles ($\chi^2 = 257$, $P < 0.001$).

Peregrine Falcon.—We found no age differences in the timing of migration in either males or females (Fig. 1, Table 1), but sample sizes for AHY are small. In 1991 through 1995 we made a special effort to identify the age of all Peregrine Falcons seen at Cedar Grove. Of the birds observed before 20 September, 24 were HY, 41 were AHY, and we were unable to determine the age of 21. Of the birds seen after 19 September, 112 were HY, 37 were AHY, and age was not determined for 85. Of the birds for which age was determined, AHY birds clearly migrated earlier than HY birds ($\chi^2 = 27$, $P < 0.001$). HY females migrated later than HY males (Fig. 1, Table 1). No sex difference was evident in the small sample of AHY birds. We trapped 15% of the Peregrine Falcons observed before 19 September, and 36% of those seen after this date, indicating that adults are much more difficult to capture than juveniles ($\chi^2 = 11.9$, $P < 0.001$).

DISCUSSION

Age differences in the timing of migration.—In fall adults (AHY) migrated later than juveniles (HY) in 8 of 10 species at Cedar Grove. Three of the eight hypotheses predict this; the social dominance hypothesis also predicts that males migrate before females, but males migrated before females in only 4 of the 22 comparisons of sexes possible in this study. The feeding efficiency hypothesis holds that juveniles migrate earlier than adults because they must migrate along with their avian prey. Of the 10 species in this study only the Sharp-Shinned Hawk and Peregrine Falcon have more than 75% birds in their diet (Snyder and Wiley 1976), and contrary to the prediction, adult Peregrine Falcons migrated before juveniles. Four of the 10 species take less than 10% birds and in 3 of these (Red-tailed Hawk, Red-shouldered Hawk, and American Kestrel) juveniles migrated before the adults. There seems to be no correlation between the prey type and early migration of juveniles. The inexperience with winter home hypothesis makes no prediction other than that juveniles migrate earlier than adults. Another possible explanation for the later migration of adults is that there is some advantage to remaining on the breeding territory as long as possible in the fall. This might facilitate early

occupancy and a better ability to defend the territory the following spring. The last two hypotheses appear to offer the best explanation as to why juveniles migrate earlier than adults in most species.

Most of the Peregrine Falcons captured at Cedar Grove are *F. p. tundrius*, which breed in the Arctic and winter to 40° S in Chile and Argentina (White 1968). The species is clearly the longest distance migratory raptor in North America. Newton (1979) noted that adult long distance migrants sometimes depart first in the autumn, travel faster, and reach the wintering areas before the juveniles. He speculated that adults might depart earlier because they are able to reach the body condition needed for migration sooner than recently fledged juveniles and might migrate faster because they know the way. Arctic breeding Peregrine Falcons have barely enough time to complete the breeding cycle before most of their prey have departed for the south (Cade 1960). As the young approach the age of independence, parent-offspring conflict (Trivers 1974) exists, and the attempts of the offspring to maximize their fitness come into conflict with that of their parents. The young selfishly demand more care than the parents should provide. As prey become scarcer, there is an increasing incentive for parents to refuse care, and we propose that the easiest way for them to do this is to leave the breeding territory before their offspring, avoiding the offsprings' incessant and aggressive begging. Alternatively, adults and juveniles may leave the breeding territory simultaneously, but adults migrate more rapidly than juveniles. Peregrine Falcons linger at Assateague Island on the Virginia and Maryland coast where the ratio of juveniles to adults is 5.7:1 (Ward et al. 1988), and at Padre Island, Texas, where the ratio is 3.9:1 (Hunt et al. 1975). The ratio at Cedar Grove, where the birds only fly past, is 1.7:1, closer to what might be expected based on the average number of young fledged and the fact that most Peregrine Falcons do not breed until they are two years old (Palmer 1988). These observations suggest that juveniles are more likely to interrupt migration in habitat suitable for hunting and thus migrate more slowly than adults.

Our results on comparisons of age agree with other studies in 18 of 24 comparisons

(Table 2). In 3 of the 6 cases that differ, the results differ significantly in one sample but not in the other. The three remaining studies indicate that juveniles migrated later than adults and our results show the opposite. The account of Kessel and Springer (1966) on Red-tailed Hawks in central Alaska is anecdotal with no data, and cannot be evaluated further. Kjellén (1992) showed that juvenile Northern Harriers and Merlins migrated significantly later than adults at Falsterbo Peninsula in southern Sweden. The data on the Merlin are questionable. Kjellén (1992) found that adult females migrated first, then juveniles of both sexes, and last adult males, with adult males and females combined migrating earlier than juveniles. Adult females are difficult to distinguish from juveniles in the hand, and we find it very hard to believe that Kjellén (1992) was able to identify similar numbers of adult females and adult males in the field. If he was incorrect in his identification of adult females, then it is possible, if not likely, that adults migrated later than juveniles. His observation that juvenile Northern Harriers migrate after adults is more difficult to dispute. Juveniles can be distinguished from adult females if a good view of the bird is obtained, and adult males are easily identified. Kjellén (1992) also presents data on age differences in the timing of migration for nine species of European raptors. The following juveniles migrated significantly earlier than adults: Red Kite (*Milvus milvus*), Marsh Harrier (*Circus aeruginosus*), and the Eurasian Sparrowhawk (*Accipiter nisus*). Adults migrated significantly earlier than juveniles among the following: Honey Buzzard (*Pernis apivorus*), Common Buzzard (*Buteo buteo*), Osprey (*Pandion haliaetus*), and Eurasian Hobby (*Falco subbuteo*). No significant age difference in the timing of migration was noted in Montagu's Harrier (*C. pygargus*) or Eurasian Kestrel (*F. tinnunculus*). Including species that also occur in North America, Kjellén (1992) found that juveniles migrated significantly later than adults in 8 species of raptors and that the opposite was true in 3 species. This ratio of 8 to 3 is a great contrast to the 1 to 8 we observed at Cedar Grove (Fisher exact test, $P = 0.01$).

Kjellén (1992) proposed that adults migrate before juveniles in long distance migrants. In

TABLE 2. Comparisons of Cedar Grove, WI, vs other studies.

Species	Citation	Locality	Finding	This study		
Northern Harrier	Bildstein et al. 1984	Duluth, MN	AHY ~ HY ^a	AHY > HY ^b		
		Hawk Cliff, ON	AHY > HY	Agrees		
		Hawk Mt., PA	AHY > HY	Agrees		
		Cape May, NJ	AHY > HY	Agrees		
		Cape May, NJ	HYF > HYM	HYF ~ HYM		
		Hawk Cliff, ON	HYF ~ HYM	Agrees		
		Duluth, MN	HYF ~ HYM	Agrees		
		Hawk Mt., PA	HYF ~ HYM	Agrees		
		Duluth, MN	AHYM ~ AHYF	Agrees		
		Hawk Cliff, ON	AHYM ~ AHYF	Agrees		
		Hawk Mt., PA	AHYM ~ AHYF	Agrees		
		Cape May, NJ	AHYM ~ AHYF	Agrees		
		Kjellén 1992	Sweden	AHYM > AHYF	AHYM ~ AHYF	
			Sweden	HY > AHY	AHY > HY	
		Northern Goshawk	Kjellén 1992	Sweden	HYM ~ HYF	Agrees
Cooper's Hawk	Dunean 1981	Hawk Cliff, ON	(HYM > HYF) ^c	Agrees		
			(AHY > HY)	Agrees		
	Delong & Hoffman 1999	Goshutes, NV & Manzanos, NM	AHYM > AHYF ^d	AHYF > AHYM		
			AHYM > AHYF	AHYF > AHYM		
			AHY > HY	Agrees		
Sharp-shinned Hawk	Rosenfield & Evans 1980	Duluth, MN	HYM > HYF	Agrees		
			(AHY > HY)	Agrees		
	Duncan 1982	Hawk Cliff, ON	(M > F)	Agrees		
			AHY > HY	Agrees		
			M > F	Agrees		
DeLong & Hoffman 1999	Goshutes, NV & Manzanos, NM	AHY > HY	Agrees			
		M > F	Agrees			
Red-tailed Hawk	Haugh 1972	Hawk Cliff, ON	(AHY > HY)	Agrees		
			ne. WI	(AHY > HY)	Agrees	
	Brinker & Erdman 1985	Cedar Grove, WI	(AHY > HY)	Agrees		
			Geller & Temple 1983	(AHY > HY)	Agrees	
Kessel & Springer 1966	cent. AK	(HY > AHY)	AHY > HY			
		(HY > AHY)	Agrees			
Red-shouldered Hawk	Dunne & Clark 1977	Cape May, NJ	(AHY > HY)	Agrees		
			Field & Field 1979	Hawk Cliff, ON	(AHY > HY)	Agrees
Rough-legged Hawk	Kjellén 1992	Sweden			HY > AHY	HY ~ AHY
			Ameriean Kestrel	Haugh 1972	Hawk Cliff, ON	(M > F)
Smallwood 1988	s. cent. FL	AHY > HY				Agrees
		Merlin	Clark 1985a	Cape May, NJ	(M > F)	Agrees
Kjellén 1992	Sweden				AHYM > AHYF	Agrees
		Peregrine Faleon	Kjellén 1992	Sweden	HY > AHY	AHY > HY
Hunt et al. 1975	Texas coast				HY > AHY	Agrees
Berry 1971	Assateague I., MD		F > M	Agrees		
			Ward et al. 1988	Assateague I., MD	(HY > AHY)	Agrees
					HY ~ AHY	HY > AHY
Kjellén 1992	Sweden	F > M	Agrees			
		HY > AHY	Agrees			

^a ~ indicates no significant difference.^b > indicates significantly later than ($P < 0.05$).^c No statistics were performed on entries in parentheses.^d Statistics performed by us.

addition to Newton's (1979) suggestion that adult long distance migrants might come into condition for migration sooner than juveniles, Kjellén (1992) proposed that adults might leave early so that more food would be available for the young, and the early arrival of the adults on the wintering area would permit acquisition of a good territory. A good winter territory would permit rapid completion of molt and accumulation of energy reserves for spring migration and the next breeding season. Adults also migrated before juveniles in 5 short distance migrants at Falsterbo. Kjellén (1992) argued that the main advantage to adults is the same as for long distance migrants: a better chance to secure a good winter territory. Juveniles migrated before adults in two short distance migrants, and Kjellén (1992) believed this is because a large part of the adult population winters close to the breeding grounds in Scandinavia, and adults either displace the juveniles or the latter are less able to cope with the reduced prey available in winter. Kjellén (1992) was unable to offer an explanation for the one remaining species (Marsh Harrier) because all individuals leave Scandinavia for southern Europe and Africa, but juveniles migrate before adults.

Our analysis of Kjellén's (1992) data fails to show relationships between which age group migrates first and the maximum distance of migration (Table 1; Mann-Whitney $U_{8,3} = 16$, $P > 0.05$), the northern ($U_{8,3} = 11$, $P > 0.05$), or the southern ($U_{8,3} = 12$, $P > 0.05$) limits of the wintering range. Adults migrate earlier than juveniles in species that breed farther north ($U_{8,3} = 2$, $P = 0.04$). The differences between Cedar Grove and Falsterbo in the timing of migration of adults and juveniles can also be explained by the northernmost latitude of breeding. Falsterbo is more than 12° latitude (about 1300 km) north of Cedar Grove and only 4 of the 10 species at Cedar Grove breed north of the latitude of Falsterbo. The relationship between maximum breeding latitude and adults preceding juveniles in Cedar Grove and Falsterbo combined is highly significant ($U_{9,11} = 2$, $P < 0.001$).

Two species occurring at Cedar Grove breed at higher latitudes than any species at Falsterbo. Peregrine Falcon adults migrate before juveniles, but there is no age difference in the timing of migration in the Rough-leg-

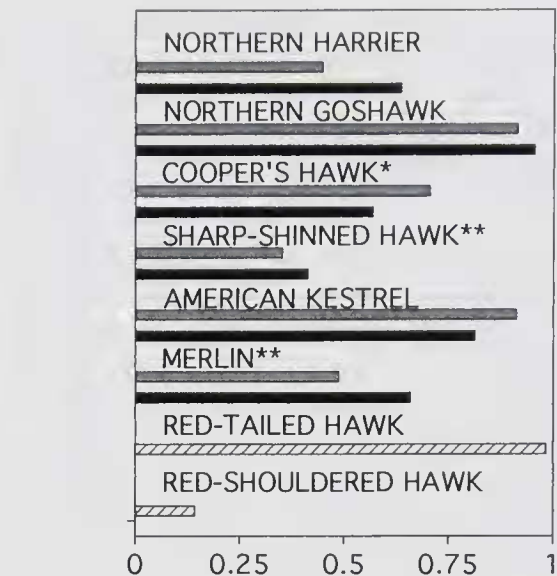


FIG. 2. Proportion of hawks with incomplete molt of remiges of rectrices during fall migration. Black bars: females. Shaded bars: males. Hatched bars: unsexed. Sex difference significant * $P < 0.05$. ** $P < 0.01$.

ged Hawk. The best explanation for early migration of adults is probably our suggestion of an early departure and more rapid migration of the adults.

Sex differences in the timing of migration.—In our study, males migrated significantly later than females in 13 of 22 possibilities, females significantly later than males in 4, and there was no significant difference between the sexes in 5 cases. Therefore, the two hypotheses that predict earlier migration of males (the social dominance and body size hypotheses) are rejected. The feeding efficiency hypothesis predicts that females migrate earlier because they are less efficient predators than males and must migrate with most of their avian prey. This hypothesis can apply to only a few species because birds are a minor component in the diet of most species. The molt hypothesis predicts that adult males migrate later than adult females but makes no prediction about juveniles. Juvenile females migrate significantly earlier than juvenile males in 7 of 10 species and adult males later than adult females in only 4 of 10 species. Incomplete molt of the remiges and rectrices was significantly more common in females than in males in 2 species (Fig. 2). Incomplete molt was significantly more common in males in only 1 species. Overall, there is little support for the molt hypothesis.

Females migrated significantly later than males in ASY Northern Goshawks and Cooper's Hawks. Newton (1979) noted that whether males or females stay on the breeding area seems to correlate with which sex is most attached to the territory; this appears to be the female in at least some species of *Accipiter*. The nesting territory of the Northern Goshawk is established and maintained by the female, and the same might be true of the Eurasian Sparrowhawk (Cramp and Simmons 1980).

We hypothesize that prolonged occupancy of the territory in autumn provides an advantage the following breeding season with the greatest advantage accruing to the sex that is the primary defender of the territory. This is usually the male but in the larger species of *Accipiter*, it appears to be the female. Several observations are consistent with the hypothesis that occupancy and defense of breeding territory are the rationale for late migration in fall. The mean difference and SD in median date of migration between the sexes in juveniles is 3.0 ± 1.73 days and for adults it is 5.9 ± 3.85 days. The difference between the two is nearly statistically significant (Wilcoxon matched-pairs signed-ranks test: $Z = 1.89$, $P > 0.05$). The mean difference in the median date of migration between adults and juveniles is 17.3 ± 10.56 days, which differs significantly from the differences between sexes in juveniles (Mann-Whitney $U_{7,7} = 4.5$, $P = 0.01$) and adults ($U_{7,7} = 9$, $P = 0.05$).

Except perhaps the American Kestrel, most individuals of most species of the raptors considered in this study probably do not breed until they are two years old (Palmer 1988). Thus, there is no reason for juveniles to delay their fall migration to occupy territories. Juvenile males migrated significantly later than juvenile females in 7 of 10 species at Cedar Grove, including the Cooper's Hawk, whose adult females migrate significantly later than adult males. Juvenile males migrate significantly earlier than juvenile females only in the Peregrine Falcon. We suggested that this species leaves the arctic breeding ground as soon as possible. Young male Peregrine Falcons fledge a mean of 3.5 days earlier than females (Sherrod 1983), and males migrate a mean of 2.3 days earlier than females.

Our results on sex differences differ from those of other studies in only 4 of 25 com-

parisons (Table 2). HY female Northern Harriers migrated significantly later than HY males at Cape May, but there was no significant difference at Cedar Grove. AHY male Northern Harriers migrated significantly later than AHY females at Falsterbo, but the difference was only marginal at Cedar Grove. AHY female Cooper's Hawks migrated significantly later than AHY males at Cedar Grove, and the opposite is true at Hawk Cliff, the Goshutes, and the Manzanos. We have no explanation for the significant disagreement between our results and those from Hawk Cliff, the Goshutes, and Manzanos.

Sex and age differences in wintering areas.—Several of the hypotheses predict age or sex differences in wintering distributions. Only a few Northern Harriers, all adult males, winter in central Wisconsin (Hamerstrom 1969). Adult males are disproportionately common around the northern Gulf of Mexico in winter (Palmer 1988). The evidence is thus inconclusive. Clark (1985b) indicated that female Sharp-shinned Hawks banded as migrants at Cape May, New Jersey, tended to winter farther north than males, but the opposite was true of birds banded at Duluth, Minnesota (Evans and Rosenfield 1985); however, an analysis of their data showed that the differences between sexes are not significant (Mann-Whitney $U_{28,73} = 1153$, $P > 0.05$, $U_{12,15} = 73$, $P > 0.05$ respectively). Although Clark (1985b) did not comment on age differences, an analysis of his data showed that there were no significant differences in the latitudinal distribution of recoveries ($U_{86,15} = 597$, $P > 0.05$). We analyzed the distributions of Sharp-shinned Hawks banded at Cedar Grove and recovered between 9 November and 15 March: 18 adult females recovered at a mean latitude of 32° , 15 juvenile females at 34° , 14 adult males at 33° , and 6 juvenile males at 31° . There are no significant differences between sexes ($U_{20,33} = 271$, $P > 0.05$) or between juveniles and adults ($U_{30,23} = 321$, $P > 0.05$).

Brinker and Erdman (1985) concluded that adult Red-tailed Hawks wintered in more northerly locations than juveniles, but an analysis of their data shows that the trend is not significant ($U_{24,33} = 345.5$, $P > 0.05$). Gauthreaux (1985) analyzed the distributions of museum specimens and found that female Rough-legged Hawks wintered significantly

farther north than males. Our data suggest that males migrate later than females, which is inconsistent with males wintering farther south. Based on 152 Christmas Bird Counts, female American Kestrels wintered significantly farther north than males (Arnold 1991). Females were significantly more abundant than males in winter in Florida, and females were significantly more abundant in the southern part of the state than in the northern part (Layne 1982). Other reports also suggest that males are more common in the northern parts of the wintering range (Mills 1975, 1976; Enderson 1960). These results are consistent with our finding that females migrate earlier than males.

The following hypotheses best explain our findings of age and sex differences in the timing of fall migration. Adults migrate before juveniles in species that breed at high latitudes because the breeding season is short and adults probably leave as soon as the young can care for themselves. The adults apparently also migrate faster than juveniles. In species breeding in more temperate latitudes, adults migrate later than juveniles because of a presumed advantage gained from remaining on territory as long as feasible. The sex that migrates later (usually the male) is the sex primarily responsible for territorial defense.

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